FAUNAL REALMS AND FACIES IN THE JURASSIC

by A. HALLAM

ABSTRACT. Differences in the composition and diversity of marine invertebrates in the Tethyan and Boreal Realms of the Jurassic are outlined, and previous interpretations based on control by temperature, physical barriers, and depth of sea are discussed and rejected. Three sedimentary facies associations, termed terrigenous clastic, intermediate, and calcareous, are distinguished in the Jurassic of Europe and a correlation with faunal realms is shown to exist. Taking this into account a hypothesis is proposed relating the establishment and maintenance of the Boreal Realm to an extensive inland sea of slightly reduced salinity in the Northern Hemisphere, which had free connections with the Tethyan and Pacific Oceans. The influence of other environmental factors and some ecological implications are briefly discussed.

SINCE the pioneer study of Neumayr (1883) it has been widely recognized that many Jurassic marine invertebrate faunas are not cosmopolitan in distribution but restricted to two or more faunal realms. The problems this has posed in stratigraphy are numerous and a correct interpretation of the causal factors is crucial to a proper understanding both of the contemporary environment and of organic evolution.

Previous workers have mainly restricted their attention to particular fossil groups, usually ammonites, and the sedimentary facies has received little attention. Consideration of data both from several major invertebrate groups and from the rocks in which they occur has led to the formulation of a new hypothesis of the origin and maintenance of Jurassic faunal realms. Arkell (1956), Imlay (1965), and Stevens (1967) review earlier work.

DISTINCTION OF FAUNAL REALMS

Of the three realms recognized by Arkell (1956, chap. 28) on the basis of ammonites, the Tethyan and Boreal Realms are accepted here as being readily distinguishable by numerous fossils from several invertebrate groups. Arkell's Pacific Realm is characterized by only a few ammonites, notably the Bajocian genera *Pseudotoites* and *Zemistephanus*, occurring with a fauna of otherwise overwhelmingly Tethyan affinities; hence I propose that it be relegated to a province of this realm.

The Boreal Realm occupies the northern part of the Northern Hemisphere. Its southern boundary is gradational and oscillated somewhat with time but generally corresponds quite closely in Europe with the line of the Alpine fold belts, and in the North Pacific region with a line through northern California and between Japan and eastern Siberia. The rest of the world belongs to the Tethyan Realm. While reading the following section documenting the differences between the two realms, it should be borne in mind that they are gradational and characterized more often by relative abundance than by complete mutual exclusion of contemporary organisms. There are many fossils, moreover, that occur commonly in both realms.

The following summary is intended to be fairly comprehensive but is far from exhaustive.

Ammonites. Because the data are relatively familiar and because of the large number of genera involved, the basic data have been condensed into a table listing only families and

B

subfamilies (Table 1). Cosmopolitan groups are excluded. This generalized picture is adequate for present purposes as long as it is borne in mind that some groups are more restricted than others. Thus the Oxfordian perisphinctids, though essentially Tethyan, range more freely into the Boreal Realm than the contemporary oppeliids; and the Toarcian Hildoceratinae, though common in the southern part of the Boreal Realm, are absent from the Arctic regions. By Tithonian/Volgian times, the ammonites of the two realms are almost totally mutually exclusive.

TABLE 1
Ammonite families and subfamilies

Stages	Boreal		Tethyan
TITHONIAN and VOLGIAN	Craspeditidae Virgatitinae		Berriasellidae Spiticeratinae Virgatosphinctinae
KIMMERIDGIAN	Dorsoplanitidae Certain Aulacostephaninae (*Aulacostephanus, Rasenia*)		Ataxioceratinae Virgatosphinctinae Simoceratidae
OXFORDIAN	Cardioceratinae		Peltoceratinae Perisphinctinae Aspidoceratinae
CALLOVIAN	Kosmoceratidae Cadoceratinae		Peltoceratinae Aspidoceratinae Reineckiidae Macrocephalitidae
BATHONIAN	Cadoceratinae		Sphaeroceratidae Tulitidae Morphoceratidae etc.
BAJOCIAN	Cadoceratinae (U. Bajocian)		Hammatoceratidae Sonniniidae Leptosphinctinae
TOARCIAN			Hammatoceratidae Bouleiceratinae
PLIENSBACHIAN	Amaltheidae Liparoceratidae		Hildoceratidae Dactylioceratidae Juraphyllitidae
SINEMURIAN and HETTANGIAN			Juraphyllitidae Ectocentritidae

(Central columns, running vertically: Oppeliidae; Phylloceratidae and Lytoceratidae)

Arkell (1956) thought that the separation into Boreal and Tethyan realms was only clearly established in the Callovian but, since the work of Callomon (1959), it has been widely recognized that a distinctive fauna of Cadoceratinae existed in the Bathonian and probably also the Upper Bajocian of the Arctic and that the Callovian marked the time of the southward spread of their descendants. Furthermore, as both Donovan (1967) and Sapunov (in press) have pointed out, the first major boreal groups are found as early as the Pliensbachian. Before this time, the Boreal Realm is generally only distinguishable as an impoverished version of the Tethyan fauna, though a number of Sinemurian genera have a predominantly northerly distribution in Europe.

Belemnites. We owe to Stevens (1965) a detailed account of world belemnite distribution. According to him, the Lias was marked only by a cosmopolitan subfamily, the Passalo-

teuthinae, but one must add here that the Triassic 'survivor' *Atractites* ranged into the Pliensbachian and is almost confined to the Tethyan Realm. A clear faunal differentiation emerged from Callovian times onwards, the Boreal Realm being characterized by species of the genera *Cylindroteuthis*, *Acroteuthis*, and *Pachyteuthis*, the Tethyan Realm by *Belemnopsis*, *Dicoelites*, *Hibolithes*, and, in the Tithonian, *Duvalia*. The post-Oxfordian restriction of some of these elements to an Indo-Pacific province need not concern us here.

Bivalves and gastropods. Most bivalves appear to be cosmopolitan in distribution but certain heavy-hinged early Jurassic genera such as *Opisoma*, *Pachymegalodon*, *Pachyrisma*, *Pachymytilus*, and *Gervilleoperna* occur only in the Tethyan Realm and the late Jurassic diceratid rudists are likewise confined. *Trigonia*, *Lithiotis*, and the peculiar pectinid *Weyla* are three other genera confined during the Lias to the Tethyan Realm.

The genus *Buchia* was formerly cited as a boreal element, because it occurs abundantly in the Arctic and in northern Europe but rarely in southern Europe. However, it has since been shown that *Buchia* occurs commonly also in the Indo-Pacific region in association with Tethyan ammonites. In the Northern Hemisphere, both *Gryphaea* and *Inoceramus* have a predominantly boreal distribution.

As regards gastropods, Imlay (1965) recognized a predominantly southern distribution of the Nerinacea, Naticacea, and Neritidae in North America. The same pattern appears to be the case in Europe, certainly for *Nerinea* and its relatives, confined to the Mediterranean countries in the Lias and predominantly Tethyan also in the Upper Jurassic (Ziegler 1964).

Brachiopods. According to Ager (1967) the most typical Tethyan brachiopods are the Pygopidae, with exaggerated anterior lobes or central perforations. Other Tethyan groups include costate terebratuloids (e.g. *Hesperithyris* in the Lias and *Flabellothyris* and *Eudesia* in the Middle Jurassic), sulcate terebratuloids, and the rhynchonellids *Prionorhynchia* and *Cirpa*, and axiniform *Zeilleria*. The Boreal Realm at this time is characterized by the dominance of *Tetrarhynchia*, *Gibbirhynchia*, *Lobothyris*, indentate *Zeilleria*, and ribbed *Spiriferina*.

Foraminifera. Many foraminifera are common in the Boreal Realm but cosmopolitan in distribution. They include the Nodosariidae (formerly grouped as Lagenidae), Ammodiscidae, and, from Middle Jurassic onwards, the Ceratobuliminidae, together with such genera as *Rheophax*, *Haplophragmoides*, *Trocholina*, *Spirillina*, *Trochammina*, and *Ophthalmidium*. Another group, belonging to the Lituolacea, is mainly or completely confined to the Tethyan Realm. This includes *Orbitopsella* (Lower Jurassic), *Orbitammina*, *Meyendorffina* (Middle Jurassic), *Pfenderina* (Middle–Upper Jurassic), and *Kurnubia*, *Anchispirocyclina*, and *Pseudocyclammina* (Upper Jurassic).

Other groups. Much attention has been paid in the past to the distribution of hermatypic corals in Europe. These exhibit a marked falling off in abundance and diversity in the late Jurassic northwards from southern regions such as Portugal, the Jura Mountains, and Swabia. The pattern of sponge distribution is similar. Groups, including algae, which appear to be mainly or exclusively Tethyan in distribution include dasycladaceans, tintinnids (first appearing in the Tithonian), coccospheres, radiolaria, and stromatoporoids.

It is a fair generalization to state that at every taxonomic level the Tethyan faunas are more diverse than the Boreal. This is well documented, for example, among cosmopolitan Liassic ammonite genera by Donovan (1967). This difference in diversity allows a distinction between the two realms to be made throughout the Jurassic, but distinctive faunal elements restricted to the Boreal Realm appear to be limited essentially to the ammonites and belemnites.

A CRITIQUE OF PREVIOUS INTERPRETATIONS

Although many environmental factors are known to influence the distribution of marine invertebrates most of these are local in effect and marine zoogeographers recognize essentially three major controlling factors on regional distribution operating at the present day; these are temperature, salinity, and physical barriers (Ekman 1953). Temperature control, of prime importance in the modern oceans, operates in restricting diversity progressively from the tropics to the poles (Fischer 1961). Salinity decrease into river estuaries and inland seas such as the Baltic and Black Seas also correlates with progressive reduction in diversity, owing to the restriction on stenohaline organisms. Physical barriers are of two sorts. Land barriers can effect a pronounced if not total separation of closely adjacent faunas. The outstanding example dates back to the mid-Tertiary, when the old Tethyan seaway, which had extended continuously across the Old and New Worlds, became divided into two by the creation of a land barrier in the Middle East, hence separating an Indo-West Pacific from an Atlantic–East Pacific Realm. Deep-sea barriers, such as that extending north and south in the East Pacific, appear to be almost as effective as land barriers in separating neritic organisms (Ekman 1953).

Regional differences in Jurassic faunas have been referred by palaeontologists to several factors, which will be discussed in turn.

Temperature. Some form of temperature control was proposed by Neumayr (1883) and Uhlig (1911) and remains the most popular interpretation among current workers (e.g. Sato 1960, Stevens 1963, 1965, 1967, Ziegler 1964, Saks *et al.* 1964, Jeletsky 1965, Donovan 1967). The evidence proposed in favour is, first, that there is a northward decrease in diversity from the Tethyan to the Boreal Realm (especially among reef corals) suggesting a comparison with climatic zonation at the present day in the Northern Hemisphere, and secondly, there is a concomitant marked decline in the abundance of limestone northwards from southern Europe.

There are a number of objections to the hypothesis of temperature control:

1. Land plant distributions reflect temperature differences and should give indication of climatic zones. Yet Jurassic plants exhibit an approach to world-wide uniformity and suggest a more equable climate than the present day. The only suggestion of climatic zonation comes from the distribution of gymnosperms in Eurasia. In the more southerly regions the flora is characterized by an abundance of cycadophytes together with conifers and subordinate gingkophytes, while the Siberian region is poorer in diversity, especially in the first-named group, and gingkophytes are more abundant (Vakhrameev 1964). Bearing in mind that living cycads characterize the tropics, this change is reasonably interpreted as controlled by climate, but the Siberian flora nevertheless signifies a humid and moderately warm climate, quite unlike the present day. In Vakhrameev's words,

'The climatic differences . . . were incomparably less sharp than the Recent epoch', and winter temperatures in Siberia could not apparently have fallen below 0 °C.

Marine invertebrates should reveal climatic differences less clearly than terrestrial plants but diversity data have been used (notably by Ziegler 1964) to support the notion of temperature control. Ziegler's data are presented in Table 2. Two further examples may be quoted here. Donovan (1967) has estimated that, among Liassic ammonite genera in Europe, 67 are chiefly or exclusively Tethyan, 30 Boreal, and 76 unrestricted. The Tithonian deposits of the Carpathians contain 30 ammonite genera (Arkell 1956) as opposed to 18 in the contemporaneous Volgian stage (as newly defined by Gerasimov and Mikhailov 1966) of the Volga Basin and Moscow region.

TABLE 2

Species of Upper Oxfordian reef corals
239 in Southern Jura
53 in Lower Saxony
13 in Southern England
7 in Yorkshire

Species of Kimmeridgian–Tithonian reef corals
113 in Portugal
143 in Württemberg
17 in Lower Saxony
1 in Normandy

Genera of Kimmeridgian ammonites
22 in Ardèche
21 in Württemberg
9 in Southern England
8 in Central European U.S.S.R.
5 in Greenland

Genera of Tithonian/Volgian gastropods
46 in Southern Jura
40 in Württemberg
17 in Southern England
13 in Central European U.S.S.R.
8 in Greenland

These figures should be compared with some Recent data, of which the best documented are those by Stehli *et al.* (1967) on bivalves. Their statistical analysis suggests that data for genera are more reliable than those for species. Within the Atlantic the generic diversity decreases northwards as follows (number of species in parentheses): Guinea Coast 92 (259), south Portugal 73 (208), south-west England 76 (180), north Scotland 46 (96), south-east Greenland 28 (57). Gradation on the western side of the Atlantic is essentially similar. There is somewhat greater diversity in the Indo-Pacific Realm, with up to 118 genera off Queensland.

In terms of degrees of latitude, Recent bivalve generic diversity decreases to approximately one-half within 50° and to one-third within 60° (if we take the Indo-Pacific values of about 120 tropical genera a change of about 50° of latitude is still required to halve the number). From 5° to 50° N. the number of genera is decreased in the Atlantic by about a quarter, the number of species by about a third.

Turning to Ziegler's data, the number of both Tithonian/Volgian gastropod and Kimmeridgian ammonite genera is reduced to less than half in a mere 5° of latitude, i.e. the northward change is much more drastic than with Recent molluscs. (Possible crustal shortening within the Alpine fold belts would affect this only slightly if at all.) On the temperature-control interpretation, this would suggest that the Jurassic climate was appreciably less, rather than more, equable than that at the present day, which seems unlikely.

Changes in faunal composition between the two realms may be equally striking over a short distance. Thus in the Lower Oxfordian Renggeri Marls of the southern French Jura, *Cardioceras* dominates in the north but diminishes to a rare element in the south, where oppeliids and phylloceratids are commoner (Enay 1966).

2. With regard to the reef corals, it is true that they are limited to the tropics today by temperature, but the present world 'model' may be inapposite for the Jurassic. Within an area where corals live today, such as the Caribbean or the Seychelles, development of coral reefs is notably patchy even in shallow water and the controlling factor on distribution can hardly be temperature, which is nearly constant; other controlling factors are important, such as turbidity, food supply, salinity, and intensity of wave exposure.

3. The distribution of limestones is a misleading guide to temperature and fails to account for the occurrence of Tethyan faunas in geosynclinal belts around the margins of the Pacific, where limestones are subordinate. Far more important than climate is the tectonic-sedimentational regime. This is true in tectonically stable as well as unstable regimes, as is clearly in evidence from the passage of shelf carbonates in the Bahamas and off southern Florida into the terrigenous clastic sequence of the Mississippi Delta, on a similar latitude. Clearly, when the clastic sequence is thicker than that of contemporary carbonate deposits the influence of river drainage should be suspected.

It is also true, however, that bed sequences in the Boreal Realm may be very condensed but still deficient in limestones. An outstanding instance is the Volgian of the Moscow region. In this case, however, modern researches on carbonate sediments indicate that they are overwhelmingly of organic origin, and temperature is not the only factor controlling the distribution of calcium carbonate-secreting organisms. Indeed, the drastic lateral passage from limestones in southern Europe to shales and sandstones in northern Europe is accomplished in only a few degrees of latitude, suggesting that some other explanation than temperature control be sought.

4. The temperature-control hypothesis, based though it is on analogy with modern climatic belts, fails to account for the lack of a distinctive Austral or Anti-Boreal fauna, and no plausible explanation has yet been offered for this. The subject is discussed more fully by Stevens (1967). The fact that certain Madagascan faunas show closer affinities to contemporaneous faunas in north-west Europe than to those in the Mediterranean region relates to sedimentary facies and cannot be construed as an argument in favour of an anti-boreal fauna in this island, because all the ammonites in question belong to the Tethyan Realm.

5. Within Europe, the transition from the Tethyan to the Boreal Realm does not relate in a simple way to latitude. Thus the Lower and Middle Jurassic faunas of the Caucasus and Turkmen, on the same latitude as the Mediterranean countries, have a notable Boreal component. While this could possibly be dismissed as due to the divergence of isotherms

from lines of latitude as at the present day, such an explanation cannot plausibly account for the fact that the Liassic ammonite fauna of the Balkan Mountains of Bulgaria is put in the Boreal Realm by both Donovan (1967) and Sapunov (in press), while a short distance to the *north-west* a typical Tethyan fauna occurs in the Bakony Mountains of Hungary. This is a serious handicap unless one accepts a drastic reshuffling of southern European fold belts such as that proposed by Carey (1958).

Physical barriers. A smaller number of authors (e.g. Uhlig 1911, Arkell 1956, Imlay 1965) have invoked some sort of physical barrier such as a land mass, as at least a contributary factor. Such an interpretation may be objected to on several grounds:

1. The changes from one realm to the other are gradational in character and there are many faunal elements common to both. This is not compatible with what is known about physical barriers in the modern oceans.

2. The boundary between the two realms oscillated geographically with time, as between the Callovian–Lower Oxfordian and Upper Oxfordian.

3. Arkell's invocation of a land barrier to isolate the Arctic Ocean and hence allow the development of a distinctive ammonite fauna in the Callovian has been rendered less plausible by the discovery of a rich boreal fauna of Bathonian Cadoceratinae in the Arctic.

4. The hypothesis suffers from vagueness. The physical barriers are usually not clearly specified nor independent evidence sought for their existence. A modified version of the hypothesis invokes ocean currents as well (Imlay 1965). This also is of doubtful significance, because the zoogeographic influence of ocean currents today is primarily one of temperature, which was probably of subordinate importance in the Jurassic.

Depth of sea. Depth is not a primary environmental factor but it often correlates with other more significant factors such as food supply, temperature, pressure, and incidence of light. There is a widespread notion, dating probably back to Haug (1907), that the phylloceratid ammonites occupied deeper water than other ammonites, hence accounting for their restriction in Europe substantially to the Mediterranean region, where rocks of supposed deep-water facies occur. A similar explanation has been tentatively proposed for certain brachiopods by Ager (1967). There may be some truth in this interpretation to the extent that, for instance, phylloceratids may dominate in beds which may reasonably be considered as having been laid down in deeper water, whereas other ammonites dominate in associated shallower-water beds, often containing algae and hermatypic corals *in situ* (e.g. Ziegler 1963). However, both types of facies occur within the Tethyan Realm and hence such data as these have nothing to do with the contrast between realms, a point well appreciated many years ago by Ortmann (1896).

It may be concluded that none of the existing explanations accounts satisfactorily for the existence of Jurassic faunal realms. Before the matter is discussed further it will be necessary to follow up a largely unheeded suggestion of Ortmann (1896), that these realms are related in some way to sedimentary facies.

JURASSIC FACIES IN EUROPE

I propose to distinguish three major marine facies associations; attention is concentrated on lithology and limited to Europe because adequate data are generally lacking from other continents.

A. *Terrigenous clastic facies association* (= Ferruginous facies of Hallam 1966)

Silty micaceous shales and siltstones with sideritic nodules, and generally subordinate fine- to medium-grained quartz sandstones and sideritic chamosite oolites, the latter representing relatively shallow-water condensed deposits. Kaolinite abundant but subordinate to illite; finely divided organic matter varies from common to uncommon; driftwood abundant; chert, red limestones, and concentrations of manganese oxide absent. Characteristic trace fossils include *Diplocraterion*, *Rhizocorallium*, and *Thalassinoides*. Abundant benthos, dominated by bivalves; faunal diversity moderate.

Examples. Most of Jurassic of Hebrides, Denmark, north Germany; much of Yorkshire Jurassic.

B. *Intermediate facies association* (= Calcareous facies of Hallam 1966)

Smooth-textured shales or marls with calcitic concretions or regular bands of fine-grained limestone; detrital quartz and mica uncommon or rare. Shallower- or more agitated-water facies represented by calcareous oolites and organic limestones containing hermatypic corals of low diversity. Poorly-aerated or anaerobic deposits represented by laminated bituminous shales. Kaolinite moderately common to uncommon, always very subordinate to illite; pyrite moderately common in shales. Chamosite and siderite rare but goethitic 'iron-shot' limestone oolites occur. Chert usually uncommon; red limestones absent. Trace fossils as for the terrigenous clastic facies association. Benthos abundant, dominated usually by bivalves; plankton usually uncommon to rare; faunal diversity moderately high.

Examples. Most of Jurassic of southern England and Paris Basin.

C. *Calcareous facies association*

1. *Shallower water.* Massive reefoid limestones with rich and diversified fossil organisms including dasycladacean algae, hermatypic corals, and stromatoporoids *in situ*, megalodontid or diceratid bivalves, etc.; associated oolites and detrital limestones; faunal diversity high.

Examples. Calcare grigi (Lias of southern Alps), Panto Crater Limestone (Lias of Greece), Plassenkalk (Upper Jurassic of Austria), much of Jurassic of central and southern Appennines.

2. *Deeper water.* Bedded fine-grained grey or white limestones with subordinate marls, replaced where sequence is condensed by red nodular limestones and marls. Intercalations of allodapic limestones (thin graded shelly beds brought in from shallower zone by turbidity currents). Chert abundant as secondary nodules or as regular beds (e.g. Malm Radiolarite of Alpine region); manganese/iron oxide incrustations common in condensed beds. Detrital quartz, kaolinite, particulate organic matter, driftwood, pyrite, chamosite, and siderite all rare or absent. Characteristic trace fossil *Zoophycos*. Benthos mostly sparse but plankton (coccoliths, radiolaria, tintinnids, etc.) abundant; faunal diversity high.

Examples. Ammonitico Rosso, Adneterkalk, Fleckenmergel, Aptychenkalk, Maiolica, Biancone, etc. of Alps and Appennines.

Facies associations A and C can be readily distinguished on lithology alone and exhibit no overlap. Chamositic ironstones are especially characteristic of the former and nodular red limestones of the latter. Towards landmasses, facies association A passes characteristically into sandy coal-measure facies (e.g. Hettangian of Scania), facies association C into calcareous, perhaps dolomitic lagoonal deposits with stromatolites and/or evaporites (e.g. Lower Purbeck Beds of southern England, Lower Lias of southern Appennines and Morocco).

It has been thought desirable to introduce a third category of facies association, B, intermediate between A and C. In certain respects, e.g. the presence of limestones, facies association B resembles C; in others, e.g. the relative abundance of clay and organic matter, it resembles A. There is the usual problem, intrinsic to all natural classifications, that any limit imposed on intergrading phenomena must be to some extent arbitrary, but facies association B should be distinguishable without difficulty provided lithological and faunal evidence are considered in conjunction. Allowing for inevitable exceptions, such as coarse clastic and volcanic deposits in the Caucasus, experience suggests that this threefold division of facies is practicable for the whole of the European marine Jurassic and provides for environmentally significant general description.

## CORRELATION OF FAUNAL REALMS AND SEDIMENTARY FACIES

When an attempt is made to plot in a generalized way the distribution of the three facies associations in Europe for particular Jurassic stages (text-figs. 1, 2, and 3, compiled from numerous sources) it becomes apparent that there is a general passage from calcareous facies association (C) in the south to terrigenous clastic facies association (A) in the north (the same is true for other stages). Since the fauna changes in the same general direction the possibility of a correlation between fauna and sedimentary facies readily suggests itself. This must therefore be examined in more detail.

The Pliensbachian stage (text-fig. 1) marks the first emergence of a major group of boreal ammonites (although not one that persisted for long) in the Jurassic. The broken line in text-fig. 1 represents the approximate boundary between Tethyan and Boreal Realms, according to data given by Donovan (1967) and Sapunov (in press). The Tethyan fauna is substantially confined to facies association C, the Boreal to facies associations A and B. The pronounced southern swing of the faunal boundary from the Carpathians to the Balkan Mountains and thence eastwards to cross between the Black and Caspian seas appears to correlate with a southward spread of facies association A in the east.

The Callovian stage (text-fig. 2) marks the time of the great 'Boreal Spread' of Arkell and shows a rather similar picture. The faunal boundary this time is taken as the southern limit of *Kosmoceras*, the most characteristic boreal ammonite genus in the European Callovian. The line is taken from Tintant (1963, fig. 86) but modified to allow for the recent discovery of *Kosmoceras* in the Balkan Mountains (Howarth and Stephanov 1965); it is closely similar to the equivalent line in text-fig. 1, and once more the correlation between fauna and facies is good, the Tethyan fauna being substantially confined to facies association C.

The Upper Oxfordian substage (text-fig. 3) was selected because it marked the time of the great 'Tethyan Spread' of Arkell, when southern elements in the ammonite fauna

spread north. It is not so easy in this case to draw a simple faunal boundary, because certain groups such as the perisphinctids, though undoubtedly Tethyan, spread further north than other, presumably less tolerant, groups such as the oppeliids. In fact the true boreal fauna, in which perisphinctids are rare or absent, is restricted to the Arctic. The line displayed in text-fig. 3, showing the approximate northern limit of abundant oppeliids, while not entirely satisfactory, is thought to be the most useful one to portray. The diagram clearly shows that there was also a notable northward migration of facies belts,
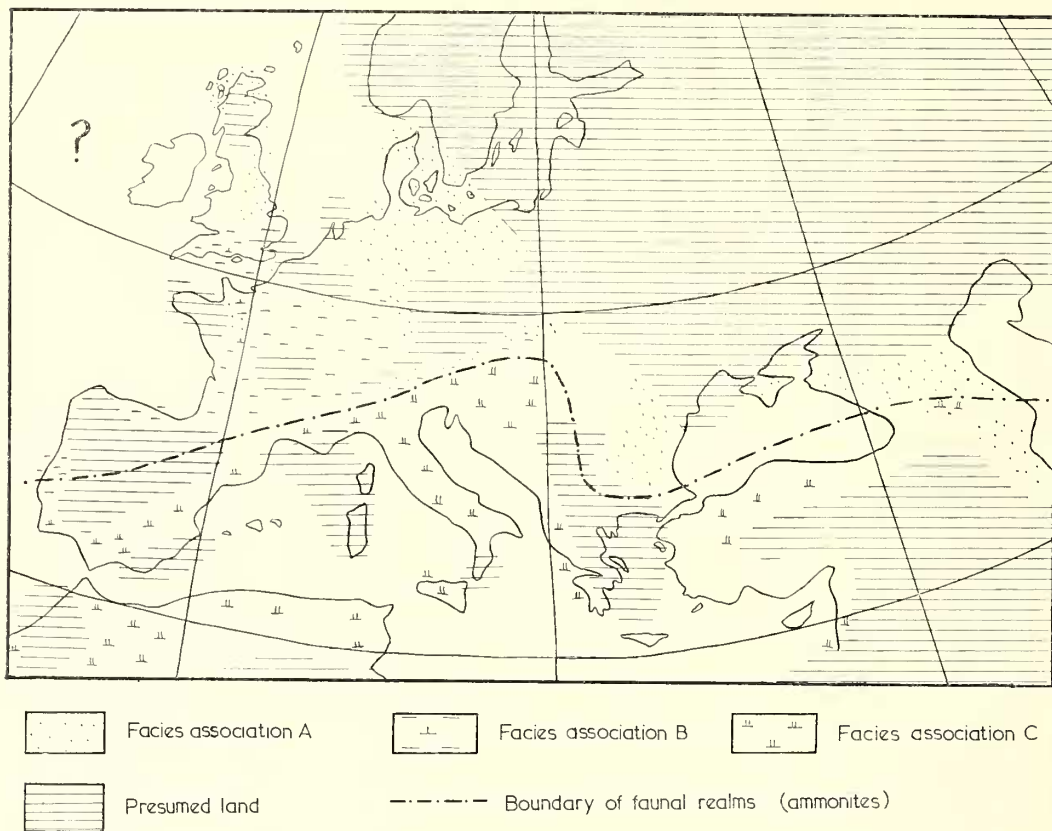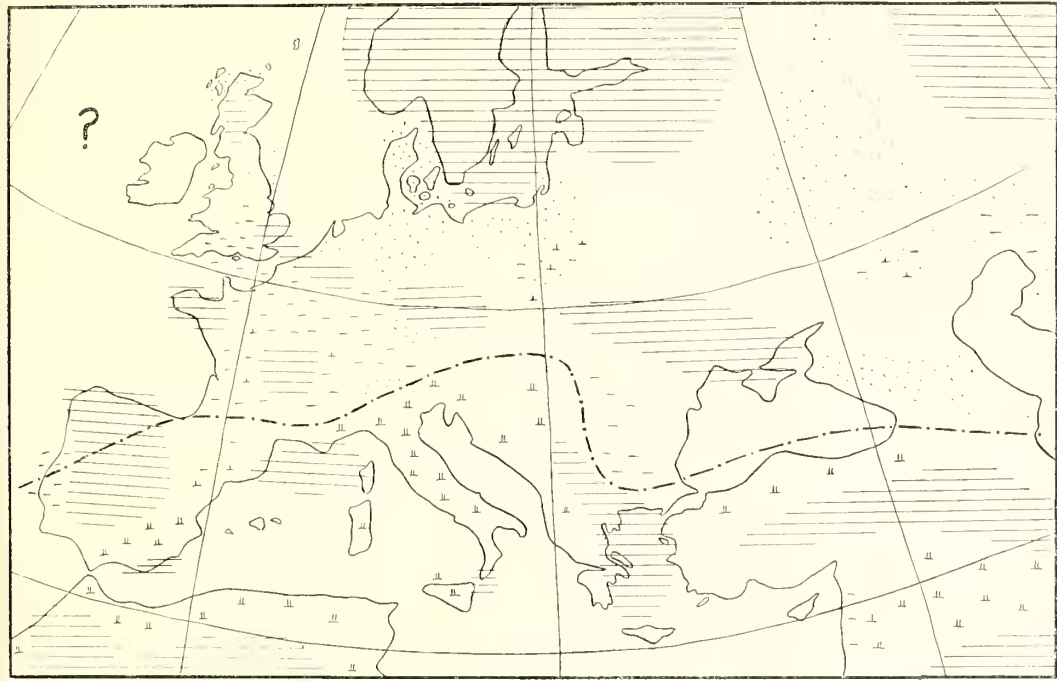

TEXT-FIG. 1. Palaeogeographic sketch map for Europe in Pliensbachian times, showing the distribution of facies associations and faunal realms.

with facies association C spreading for the first time far into Central Europe, and facies association B being in general more calcareous than the equivalent facies in the underlying Callovian and Lower Oxfordian. A map for the Lower Kimmeridgian would show a further Boreal Spread of ammonites and other fossils (Arkell 1956, Ziegler 1964), correlating with a southward shift of facies belts, most notably in north-west Europe.

It is clear therefore that there is a good general correlation, both in space and time, between the ammonite fauna and facies, and the same holds true for other groups, i.e. facies association C of southern Europe belongs to the Tethyan Realm, facies association

A in northern Europe to the Boreal Realm. The question arises whether this correlation also applies in detail, because the maps are too generalized to take account of small-scale variations. A close study of regional and sequential facies variations in the Upper Pliens-bachian and Lower Toarcian within one country (Hallam 1967b) reveals a good cor-relation in both space and time. Southwards in England, the sedimentary facies changes in the direction A to B and Tethyan elements in the molluscs and brachiopods occur in the extreme south. The change from Pliensbachian to Toarcian is marked by a wide-

—·—·—·— Southern boundary of Kosmoceras

TEXT-FIG. 2. Palaeogeographic sketch map for Europe in Callovian times. Explanation as in text-fig. 1.

spread change from facies association A to B and correlates with a 'Tethyan Spread' of ammonites. Another English example is shown in the transition from the Bathonian to the Callovian. South of Yorkshire a calcareous version of facies association B, with ammonites of Tethyan affinities, passes up into more sandy and argillaceous strata containing Boreal ammonites.

INTERPRETATION

Marine zoogeographers consider salinity to be one of the major factors controlling regional distribution of fauna, yet this has never been seriously considered to be relevant in accounting for Jurassic faunal realms. There are, however, a number of grounds for considering salinity to be a major influence:

1. The pattern of sedimentary change in Europe from calcareous (C) via intermediate (B) to terrigenous clastic (A) facies associations is best explained as a consequence of

passage from a pelagic or oceanic environment in a locally shallow and never especially deep sea towards a non-pelagic environment under the strong influence of rivers. This interpretation has previously been considered in some detail (Hallam 1967a, b) and consequently need only be referred to briefly here. The rivers brought into the marine environment quantities of quartz/feldspar sand and silt together with clay including substantial quantities of kaolinite; also iron, in dissolved or suspended form, and plant matter. Phytoplankton flourished in the inshore zone, partly as a result of the influx of
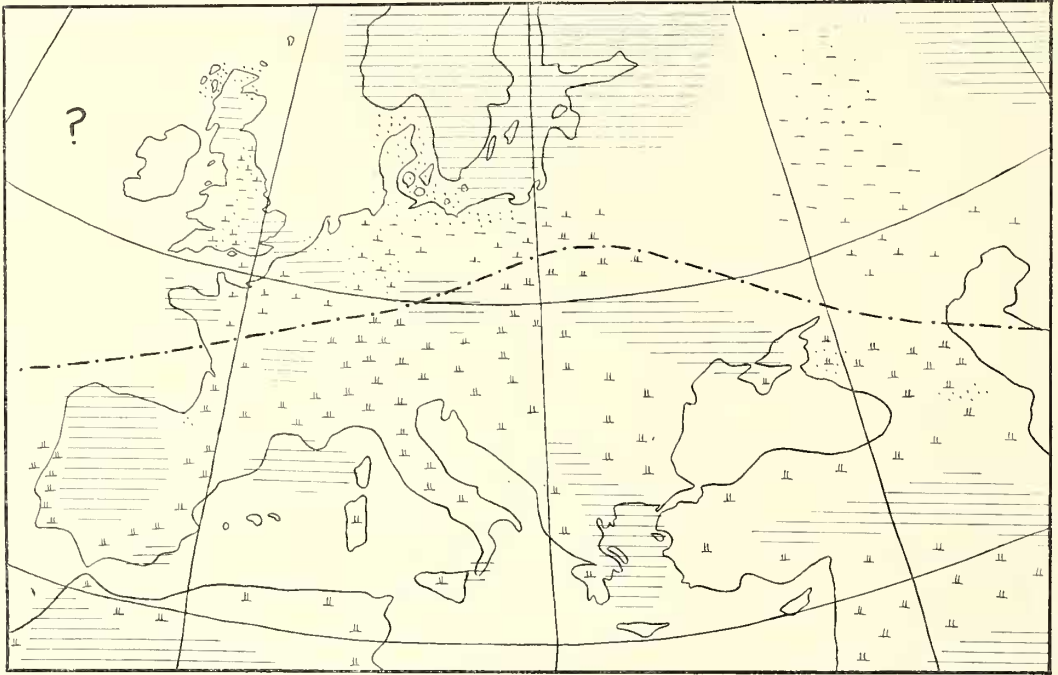
— · — · — · —   Northern boundary of abundant oppeliids

TEXT-FIG. 3. Palaeogeographic sketch map for Europe in Upper Oxfordian times. Explanation as in text-fig. 1.

nutrients from the land. The presence of red limestones and manganese concentrations in condensed beds in the calcareous facies association relates to the relative sparsity of organic matter in the oceanic environment. Salinity of the inland sea or 'inshore' region must have been lowered somewhat by the influx of fresh water from the land and the good correlation that appears to exist between litho- and biofacies points to the operation of this factor in controlling faunal distribution.

2. Besides temperature, salinity is effectively the only major inorganic factor that can produce such faunal diversity gradients on a regional scale. The nature of the diversity contrast between the Tethyan and Boreal realms accords with the salinity-control hypothesis in that the greatest diversity is found in the pelagic environment. Moreover, among the organisms with close relatives surviving today, it is notable that representatives of the bivalves, gastropods, ostracods, and agglutinating foraminifera with simple

structure flourished in the Boreal Realm, as they do in present-day seas with reduced salinity. On the other hand, known stenohaline groups such as the hermatypic corals were very largely confined to the Tethyan Realm. Dasycladacean and other types of benthonic lime-secreting algae were, like the planktonic coccospheres, largely confined to the normal salinities of the open sea. Now that electron microscopy has revealed that many Upper Jurassic fine-grained limestones in the Mediterranean region contain numerous coccoliths (Garrison 1967, Farinacci 1964, Flügel 1967) there is an explanation of why limestone is sparse even in condensed clay sequences in the Boreal Realm. Likewise, the restriction of diagenetic chert mainly to facies association c correlates with the occurrence in abundance of calcitized radiolaria and siliceous sponges.

TABLE 3

	Kattegat	Belt Sea	Arkona Sea	Gulf of Finland
Salinity of bottom waters	c. 35‰	25–30‰	10–15‰	5‰
No. of species of bivalves	92	34	24	4
„ „ polychaetes	193	143	15	3
„ „ crustaceans	232	97	29	11
„ „ fish	75	55	30	22
Total species	592	329	98	40

The best-documented example of salinity gradients in modern seas is that of the Baltic Sea. Table 3 is compiled from Segerstråle (1957, table 2, and fig. 2). Segerstråle recorded a 'filtering out' of stenohaline groups such as coelenterates, brachiopods, cephalopods, radiolaria, and echinoderms and a reduction in the diversity of more tolerant groups passing eastward into the Baltic from the North Sea. It will be noted from Table 3 that even the euryhaline groups exhibit a large reduction in numbers of species with only a small change of salinity; thus a drop of only 5–10‰ correlates with a reduction in species number by almost a half. If stenohaline groups are included then the reduction is by much more than a half.

3. The faunal abundance (for a given thickness of deposit) is usually, in contrast to the diversity, greater in the Boreal Realm. This is true especially of the bivalves. Genera such as *Buchia*, *Inoceramus*, and *Gryphaea* often occur in large quantities in faunas of quite low diversity. This phenomenon exactly parallels the situation in modern estuaries and inland seas, where the abundant food supply favours mass colonization by those organisms that can survive the reduced salinity.

4. Wall (1965) described non-calcareous microplankton of Liassic Beds in Britain (Boreal Realm) that are low in diversity, associated with pollen and spores of greater diversity; he interpreted these facts to signify that the environment was an inshore one, with close proximity to coastal vegetation.

5. At the present day (Bandy 1960) agglutinating foraminifera with a simple shape are characteristic of bays and lagoons, whereas labyrinthine forms and those with siphonate chambers are found in the central and outer parts of shelf areas and the bathyal zone.

This accords precisely with the salinity-control hypothesis for the Jurassic. Simple agglutinating foraminifera such as *Ammodiscus*, *Ammobaculites*, *Hyperammina*, and *Rheophax* are among the few faunal elements that occur in marginal marine–continental clastic deposits of the sort that pass laterally into coal measures

(Kaptarenko-Tschernousowa 1964). On the other hand, complex forms belonging to the Lituolacea are characteristic of, and mainly restricted to, the Tethyan Realm.

It may be objected that the Boreal Realm, with its abundant echinoderms, cephalopods, and brachiopods, which are all stenohaline groups judging from their present-day distribution, signifies marine rather than brackish-water conditions. This, while perfectly true, does not affect the argument, since what is envisaged is an extensive inland sea with only slightly reduced salinity, unlike the eastern Baltic or Black Seas. Echinoderms, in fact, are more tolerant of salinity than is generally realized and Binyon (1966) lists seventeen species that are known to survive in waters of less than 20‰. Cephalopods and brachiopods are undoubtedly less tolerant, but in both cases species are known that can survive in waters down to about 30‰ (Mangold-Wirz 1963, Cori 1933). This difference in tolerance probably helps to account for the fact that a number of echinoderms are known from the Rhaetic in England (H. Ivimey Cook, personal communication), having entered the succession earlier than the first cephalopods and brachiopods which first appear a short distance above the base of the Lias. This accords well with the usual palaeogeographic notion of a slowly transgressing sea bringing progressively increasing marine influence to this region.

Taking into account the Baltic Sea data, it is clear that even a slight reduction in salinity can exert strong influence on the fauna and that the Jurassic diversity data are more plausibly explained by this means than by the only reasonable alternative, temperature.

It is not difficult to show, however, that salinity could not have been the only factor responsible for the differentiation of faunal realms. The relatively straight-forward relationship that exists between litho- and biofacies throughout Europe outside the Caucasus breaks down in the unstable eugeosynclinal belts, where Tethyan faunas occur in terrigenous and volcanic clastic facies, locally passing into continental coal measures. Even in tectonically stable zones undoubted brackish-water faunas occur locally within the Tethyan Realm. Evidently the general palaeogeographic setting must be taken into account, for the Boreal Realm needed both space and time to develop; mere local reduction in salinity was not enough. In other words, it is necessary to invoke an extensive area of relatively stable palaeogeography where an inland sea of slightly reduced salinity (perhaps on average down to about 30‰) could persist long enough to allow a separate fauna (derived from some Tethyan ancestors) to evolve unmolested, being protected from biological competition by a 'salinity bar'. This may well account for the progressive differentiation of a boreal fauna of ammonites and belemnites (marked by a false start, i.e. the liparoceratid–amaltheid lineage which became extinct at the close of the Pliensbachian) which correlates with the progressive transgression of the Jurassic seas that continued at least until late Oxfordian times. This gradual transgression, which can be discerned despite local tectonic disturbances and minor oscillations, caused a progressively larger area of a boreal continent to be flooded, so expanding the 'niches' available for colonization. Arkell's two 'boreal spreads', in the Callovian and Lower Kimmeridgian, which can also be recognized in western North America (Imlay 1965), correlate in Europe with a southward migration of terrigenous clastics presumably related to tectonic uplift in the north. The Upper Oxfordian marks the time when the Jurassic transgression reached its climax and the Tethyan fauna achieved its greatest extent as river mouths were pushed back.

The sort of palaeogeography envisaged is represented diagrammatically in text-fig. 4. I consider on independent grounds that the Atlantic Ocean probably did not exist during the Jurassic. While not crucial to the interpretation proposed above, it appears more plausible if there were only one northern continent rather than two, since this allows for the extensive development of a shallow boreal inland sea with free oceanic connections but persistently kept at a slightly lower salinity. This indicates a humid climate, with abundant freshwater run-off from the well-vegetated northern land masses emergent from this inland sea. The sparsity of terrigenous clastics further south is clearly a function of reduced river influence but land was not necessarily distant (text-fig. 4). Perhaps the climate further south was more arid, a suggestion which is supported by the widespread occurrence of evaporites in lagoonal deposits associated with the calcareous facies.
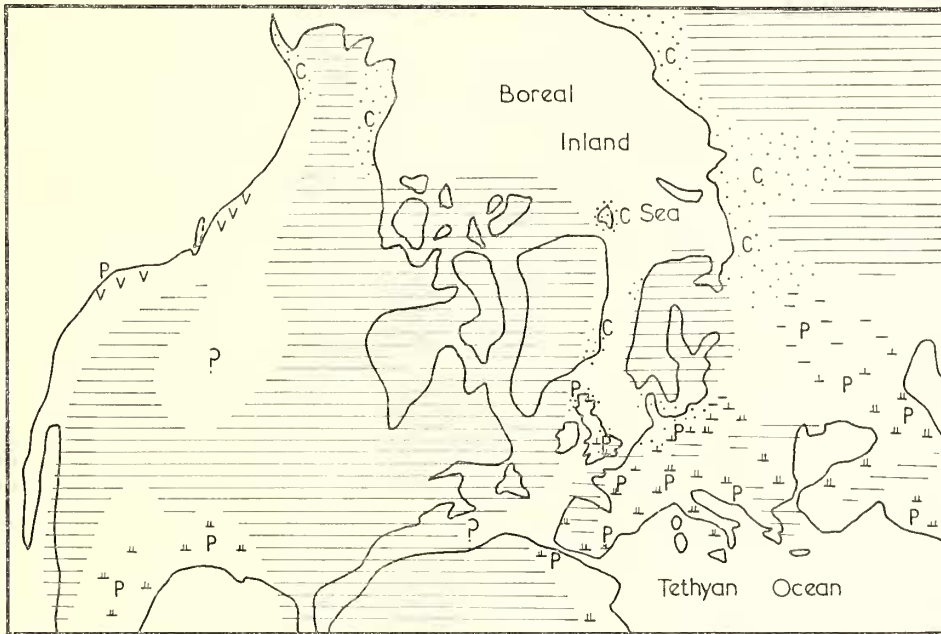
TEXT-FIG. 4. Proposed Upper Oxfordian palaeogeography for the northern hemisphere, using the fit of the Atlantic continents suggested by Bullard *et al.* 1965. Explanation as in text-fig. 1. P = Perisphinctacea common, C = Cardioceratinae dominant, perisphinctids absent or subordinate; V = volcanic–clastic beds of West Cordilleran geosyncline.

Did climate play no role other than this? There is, of course, no denying that on astronomical grounds temperature must have been higher at the equator than at the poles. It is my contention, however, that the difference was too slight to have had more than, at most, a minor influence on the faunal distributions. In so far as there would have been a temperature gradient from south to north, its effect would have served to reinforce that due to salinity. Thus, Arctic Callovian faunas are dominated by *Cadoceras* rather than the common European genus *Kosmoceras*, and other Arctic faunas often show lower

diversity than those in Europe. Such differences as these could possibly be the consequence of a slight temperature gradient.

Turbidity and food supply are other factors which should not be ignored. They might, for instance, help to account for the abundance of *Buchia* in Oxfordian and younger Jurassic deposits wherever the rocks are rich in terrigenous clastics, regardless of whether the associated fauna is Tethyan or Boreal.

Finally, there is the possibility of biological competition. Once a boreal fauna was established, elements of the Tethyan fauna might have been prevented from entering the Boreal Realm even though they could tolerate the lowered salinity. A possible example concerns the coexistence during the late Pliensbachian of amaltheids in the Boreal and hildoceratids and dactylioceratids in the Tethyan Realm. Not until after the amaltheids died out was there a significant extension of the other families into the Boreal Realm. This was probably due at least in part to the Toarcian transgression but biological competition may also have played a role.

The hypothesis that finally emerges obviously involves rather more than simple salinity control, but I believe this to be by far the most important environmental variable, apart from palaeogeographic configuration. To test the hypothesis adequately in detail, many more data need to be amassed on relative faunal abundances and associated lithology than are currently available.

In conclusion, a few ecological implications can be suggested. There is a tendency for Jurassic cephalopods to fall into two categories which may be called pelagic (or stenohaline) and non-pelagic (slightly euryhaline). This finds a parallel among living cephalopods (Mangold-Wirz 1963). Among the pelagic group, the phylloceratids and lytoceratids probably had a wider depth range than other ammonites such as the oppeliids, judging from their facies distribution in southern Europe, as documented for instance by Ziegler (1963). Among the benthos, brachiopods are relatively more important in the 'deeper water' calcareous facies than bivalves, in contrast to the shallower-water facies of the Boreal Realm. This may well signify better adaptation among characteristic Tethyan brachiopods to relative sparsity of food, as indeed Vogel (1966) has argued specifically in the case of *Pygope*. As already indicated, however, it is not necessary to invoke water of any great depth. Likewise, the organism that produced the characteristic Tethyan trace fossil *Zoophycos*, clearly a systematic sediment-feeder, was probably better adapted to a limited food supply than the organisms responsible for the common trace fossils of the Boreal Realm.

REFERENCES

AGER, D. V. 1967. Some Mesozoic brachiopods in the Tethys region. *Systematics Ass. Publ.* **7**, 135–50.
ARKELL, W. J. 1956. *Jurassic geology of the world.* Edinburgh.
BANDY, O. L. 1960. General correlation of foraminiferal structure with environment. *Rep. 21st Int. geol. Congr.*, part 22, 7–19.
BINYON, J. 1966. Salinity tolerance and ionic regulation. In BOOLOOTIAN, R. A., (ed.) *Physiology of Echinodermata*, 359–77. New York, etc.
BULLARD, E. C., EVERETT, J. E., and SMITH, A. G. 1965. The fit of the continents around the Atlantic. *Phil. Trans. R. Soc.* **258A**, 41–51.
CALLOMON, J. H. 1959. The ammonite zones of the Middle Jurassic beds of East Greenland. *Geol. Mag.* **96**, 505–13.

CAREY, S. W. 1958. A tectonic approach to continental drift. *Geol. Dept. Univ. Tasmania, Symp.* **5**, 177–355.

CORI, C. I. 1933. Brachiopoda. In: *Die Tierwelt der Nord- und Ostsee*, teil 7, c. 3, lief. 24, 133–50, Leipzig.

DONOVAN, D. T. 1967. The geographical distribution of Lower Jurassic ammonites in Europe and adjacent areas. *Systematics Ass. Publ.* **5**, 111–32.

EKMAN, S. 1953. *Zoogeography of the sea.* London.

ENAY, R. 1966. L'Oxfordien dans la moitié sud du Jura français—étude stratigraphique. *Nouv. Arch. Mus. His. nat. Lyon*, fasc. VIII, **1**, 2.

FARINACCI, A. 1964. Microorganismi dei Calcari 'Maiolica' e 'Scaglia' osservati al microscopio elletronico (Nannoconi e Coccolithophoridi). *Boll. Soc. Paleont. Ital.* **3**, 172–81.

FISCHER, A. G. 1961. Latitudinal variations in organic diversity. *Am. Scientist*, **49**, 50–74.

FLÜGEL, E. 1967. Elektronenmikroskopische Untersuchungen an mikritischen Kalken. *Geol. Rdsch.* **56**, 341–58.

GARRISON, R. E. 1967. Pelagic limestones of the Oberalm Beds (Upper Jurassic–Lower Cretaceous), Austrian Alps. *Bull. Canad. Petrol. Geol.* **15**, 21–49.

GERASIMOV, P. A. and MIKHAILOV, N. P. 1966. The Volgian stage and the standard scale for the upper series of the Jurassic System. *Izv. Akad. Nauk SSSR, ser. geol.* **2**, 118–38 (in Russian).

HALLAM, A. 1966. Depositional environment of British Liassic ironstones considered in the context of their facies relationships. *Nature, Lond.* **209**, 1306–7.

—— 1967a. Sedimentology and palaeogeographic significance of certain red limestones and associated beds in the Lias of the Alpine region. *Scot. J. Geol.* **3**, 195–220.

—— 1967b. An environmental study of the Upper Domerian and Lower Toarcian of Great Britain. *Phil. Trans. R. Soc.* **252B**, 393–445.

HAUG, E. 1907. *Traité de géologie.* Paris.

HOWARTH, M. K. and STEPHANOV, J. 1965. The genus *Kosmoceras* in Bulgaria. *Bulg. Akad. Nauk, Geol. Inst., Tr. Geol. Bulg., Ser. Pal.* **7**, 135–49.

IMLAY, R. 1965. Jurassic marine faunal differentiation in North America. *J. Paleont.* **39**, 1023–38.

JELETZKY, J. A. 1965. Late Upper Jurassic and early Lower Cretaceous fossil zones of the Canadian Western Cordillera. *Bull. Geol. Surv. Can.* **103**.

KAPTARENKO-TSCHERNOUSOWA, O. K. 1964. Versuch eines stratigraphisches Vergleiches der Jura-Ablagerungen auf Grund ihrer Foraminiferen-Fauna. 1ᵉ Colloque Jurass. Luxemb. *Publ. Inst. gr. ducal, Sect. sc. nat., phys. math.* 429–37.

MANGOLD-WIRZ, K. 1963. Biologie des cephalopodes benthiques et nektoniques de la Mer Catalane. In '*Vie et Milieu*', *Publ. Lab. Arago*, Univ. Paris, suppl. **13**.

NEUMAYR, M. 1883. Über klimatische Zonen während der Jura- und Kreidezeit. *K. Akad. Wiss. Wien Denkschr., Math-naturh. Kl.* **47**, 277–310.

ORTMANN, A. E. 1896. An examination of the arguments given by Neumayr for the existence of climatic zones in Jurassic times. *Am. J. Sci.* 4 ser. **1**, 257–70.

SAKS, V. N., MESEZHNIKOV, M. S., and SHULGINA, N. I. 1964. About the connection of the Jurassic and Cretaceous marine basins in the north and south of Eurasia. *Dok. Sovetsk. Geol. Mezh. Geol. Kong. 22nd Ser.* 163–74 (in Russian).

SAPUNOV, I. G. (in press). Notes on the geographic differentiation of the Lower Jurassic faunas. *2ᵉ Colloque Jurass. Luxemb.*

SATO, T. 1960. A propos des courants oceaniques froids prouvés par l'éxistence des ammonites d'origine arctique dans le Jurassique japonais. *Rep. 21st Int. geol. Congr.* part 12, 165–9.

SEGERSTRÅLE, S. G. 1957. Baltic Sea. *Mem. geol. Soc. Am.* **67**, 1, 751–800.

STEHLI, F. G., MCALESTER, A. L., and HELSLEY, C. E. 1967. Taxonomic diversity of Recent bivalves and some implications for geology. *Bull. geol. Soc. Am.* **78**, 455–66.

STEVENS, G. R. 1963. Faunal realms in Jurassic and Cretaceous belemnites. *Geol. Mag.* **102**, 175–8.

—— 1965. The Jurassic and Cretaceous belemnites of New Zealand and a review of the Jurassic and Cretaceous belemnites of the Indo-Pacific region. *Bull. geol. Surv. N.Z. Palaeont.* **36**.

—— 1967. Upper Jurassic fossils from Ellsworth Land, West Antarctica, and notes on Upper Jurassic biogeography of the South Pacific region. *N.Z. Journ. Geol. Geophys.* **10**, 345–93.

TINTANT, H. 1963. Les Kosmoceratides du Callovien inférieur et moyen d'Europe occidentale. *Dijon Univ. Publ.* **29**.

UHLIG, V. 1911. Die marinen Reiche des Jura und der Unterkreide. *Mitt. Geol. Gesell. Wien*, **4**, 329–448.
VAKHRAMEEV, V. A., 1964. Jurassic floras of the Indo-European and Siberian botanical-geographical regions. 1ᵉ Colloq. Jurass. Luxemb. *Publ. Inst. gr. dnc Lnxemb. Sect. Sci. nat., phys. math.* 411–21.
VOGEL, K. 1966. Eine funktionsmorphologische Studie an der Brachiopodengattung *Pygope* (Malm bis Unterkreide). *Neues Jb. Geol. Paläont. Abh.* **125**, 423–42.
WALL, D. 1965. Microplankton, pollen and spores from the Lower Jurassic in Britain. *Micropaleontology*, **11**, 151–90.
ZIEGLER, B. 1963. Die Fauna der Lemeš-Schichten (Dalmatien) und ihre Bedeutung für den mediterranen Oberjura. *Nenes Jb. Geol. Paläont. Mh.* **8**, 405–21.
—— 1964. Boreale Einflüsse im Oberjura Westeuropas? *Geol. Rdsch.* **54**, 250–61.

A. HALLAM
Department of Geology and Mineralogy
University of Oxford

Typescript received 3 April 1968